DIFFERENTIAL PERFORMANCE OF A *CONTARINIA* GALL MIDGE (DIPTERA: CECIDOMYIIDAE) ON ANT-DEFENDED *ACACIA CORNIGERA* (FABACEAE)

ZHIWEI LIU AND HORACIO BONFIL

(ZL) Department of Entomology, Swedish University of Agricultural Sciences, Box 7044, S-750 07 Uppsala, Sweden; Division of Invertebrate Zoology, American Museum of Natural History, New York, NY 10024, U.S.A.; current address: Division of Insects, Field Museum of Natural History, Chicago, IL 60605, U.S.A. (e-mail: zliu@fmnh.org); (HB) Center of Ecology, National University of Mexico, P.O. Box 70-275, Ciudad Universitaria, 0410, D.F., Mexico

Abstract.—Galls induced by an unidentified species of *Contarinia* gall midge were found on leaves of *Acacia cornigera* L. in Los Tuxtlas, Veracruz, Mexico. The host plant is protected against other herbivores by the mutualistic ant species *Pseudomyrmex ferrugineus* (Smith). We found that the density of the galls was significantly different among *A. cornigera* trees with different functional categories of ant colonies, as determined by the colonies' development stages. The galls were also unevenly distributed among positions within leaves. More leaves were galled on the rachis and pinna than at other positions, but galls at the leaf base and extrafloral nectary were larger than those on the rachis or pinna. No difference was found for parasitism of mature galls by parasitic wasps between the trees with different functional categories of ant colonies. We conclude that ant protection of acacia trees may be effective against specialized herbivores like gall-makers. A trade-off may exist for the gall midge in that gall size is largest at leaf positions where risk of predation is greatest, creating the uneven distribution of galls among leaf positions. The hypothesis that the gall midges of *Contarinia* sp. may benefit by living in 'enemy-free space' created by the ant is not supported by the present study.

Key Words: *Acacia cornigera,* ant protection, *Contarinia,* Cecidomyiidae, enemy-free space, gall makers, mutualism, parasitism, *Pseudomyrmex ferrugineus*

The relationship between *Pseudomyrmex* spp. and *Acacia* spp. has been widely cited as obligate mutualism (Futuyma 1986, Huxley and Cutler 1991, Hölldobler and Wilson 1990, Krebs 1994). The ant-acacia tree provides the ant with hollow thorns as nesting sites, and Beltian bodies and extrafloral nectar as food. The ant, in return, provides the tree with protection against herbivores. Several ant-acacias have lost the chemical traits that protect other *Acacia* species from herbivores (Rehr et al. 1973, Seigler et al. 1978, Seigler and Ebinger 1995). Field experiments have shown that acacia trees grow less and are frequently killed when deprived of ant protection (Janzen 1966, 1967). Similar associations have also been reported for other myrmecophytic plants associated with ants (Longino 1991, Fowler 1993, Fonseca 1994).

The insect fauna associated with myrmecophytic plants is usually less diverse and less abundant, and consists of more specialized species compared to non-myr-

mecophytic plants (Jolivet 1991). Some specialists are able to circumvent ant attack through fast escape, building shelters or making galls (Heads and Lawton 1985, Koptur 1992, Loeffler 1996, Eubanks et al. 1997). Such insects may even take advantage of the fact that their natural enemies may be chased off, thereby living in 'enemy-free space' created by the ants (Koptur 1991, 1992). For shelter-builders and gall-makers, however, the ant threat still exists for egg-laying females and the life stages not yet concealed, such as eggs and young larvae. Ants may actively remove those exposed insects from their host plant surface (Stephenson 1982, Fiala et al. 1991).

In Los Tuxtlas, Mexico, two major specialist herbivores were found on *Acacia cornigera* L., which harbored the obligate mutualistic ant *Pseudomyrmex ferrugineus* (Smith). The larva of *Polyhymno* sp. (Lepidoptera: Gelechiidae), a shelter builder, can defeat the ant-defense of *A. cornigera* and inflict mortality-level defoliation on the host plant (Eubanks et al. 1997). The other, *Contarinia* sp., is a cecidomyiid fly that makes galls on the plant, mostly on the leaves.

According to our preliminary observations, the leaf galls at extrafloral nectaries appeared to be larger than those at other positions of the leaves. In many systems, large galls not only produce large adults with high fecundity (Weis et al. 1988), but also provide better protection against natural enemies such as parasitoids (Price and Clancy 1986, Weis et al. 1988). Thus, the gall inducer may prefer to lay more eggs at extrafloral nectaries. However, these positions are also resources for, and frequently visited by, both the ants and generalist parasitoids (Koptur 1991), and therefore represent a risk for the gall-maker as well.

The present study was designed to examine the *Acacia*-ant cecidomyiid interactions. Specifically, the following questions were asked: (1) Does the presence of ants significantly reduce herbivory inflicted on *Acacia* trees by specialized herbivore insects such as gall-making cecidomyiids? (2) Are galls evenly distributed among leaf positions and what role, if any, do the ants and parasitic wasps play in determining such a pattern? (3) Do the gall midges gain protection from the ants against parasitic wasps, thus living in 'enemy-free space'?

Natural History

Host plant.—*Acacia cornigera* L. (Leguminosae: Mimosaceae) is naturally distributed in wet to relatively dry, mostly disturbed habitats at lower elevations from southern Mexico to Costa Rica (Seigler and Ebinger 1995). At the base of each compound leaf is a pair of thorns, which are modified stipules. The thorns are excavated and occupied by the ants when the thorns are still very young (Liu, personal observation). The compound leaf consists of petiole, rachis, pinna, and pinnules or leaflets. The Beltian bodies are located at the tips of the pinnules of young leaves (Fig. 1), but are rarely seen because they are usually harvested by the ants as soon as the young leaves develop (Seigler and Ebinger 1995). Extrafloral nectar is produced on a continuous basis by canoe-shaped nectaries on the dorsal side of the petiole and, rarely, also on the rachis (Janzen 1966, 1967, 1974; Seigler and Ebinger 1995; Liu, personal observation).

Associated ant species.—*Pseudomyrmex ferrugineus* (Smith) (Hymenoptera: Formicidae), often erroneously cited as *P. ferruginea* (e.g., Janzen, 1966, Mintzer et al., 1987, but see Ward, 1989, 1993), has become well known because of Janzen's studies (1966, 1967), which provided strong experimental evidence for the mutualism between the ant and *Acacia cornigera*. It has a distribution ranging from eastern and southern Mexico to El Salvador and Honduras. It is a common species and uses as domatium hosts all swollen-thorn acacia species growing within its range, including *Acacia chiapensis, A. collinsi, A. cookii, A. cornigera, A. gentlei, A. globulifera, A. hindsii, A. janzenii, A. mayana,* and *A.*
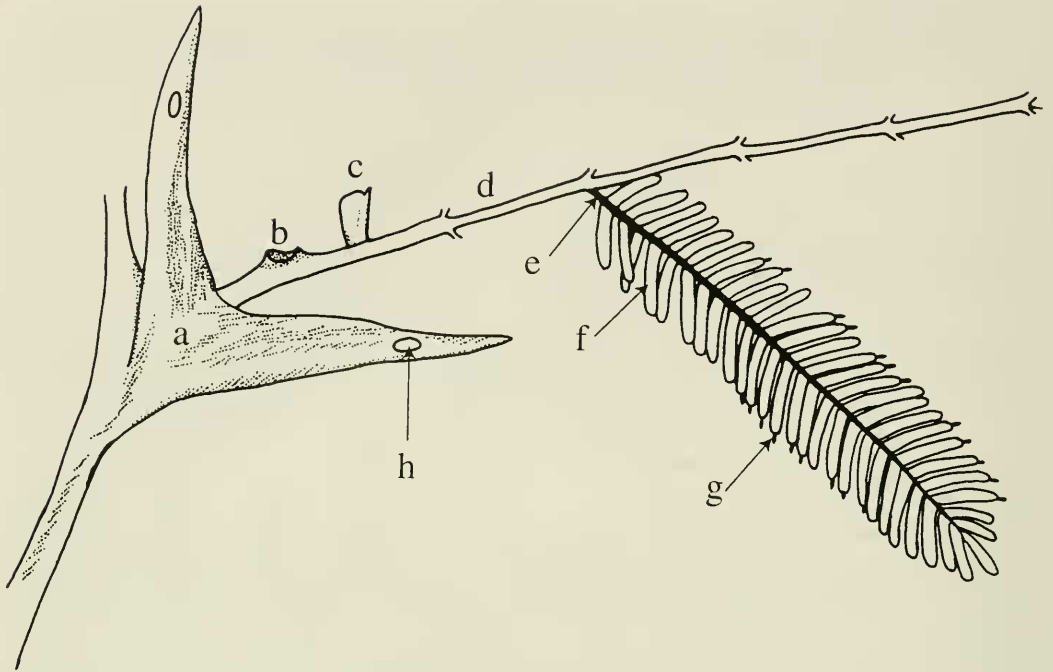
Fig. 1.   Diagram of a branch of ant acacia, *Acacia cornigera,* with *Contarinia* sp. gall (a = thorn; b. = nectary; c = gall induced by a *Contarinia* gall midge; d = rachis; e = pinna; f = pinnule; g = Beltian body; h = ant exit.

sphaerocephala (Ward 1993). *Pseudomyrmex ferrugineus* resides in the thorns of the acacias. Usually only one colony exists in an acacia tree. Workers of young colonies leave the thorns only long enough to collect nectar and Beltian bodies, but they begin patrolling the plant surface when the colony has reached a size of 50–100. When ant numbers reach 200–400, the workers become more aggressive and start attacking competing ant colonies, as well as warding off other insects that attempt to land in the vicinity. It takes about 10 months for an ant colony to reach this stage (Janzen 1967). Janzen (1967) classifies the ant colonies into three functional categories on the basis of their developmental stages: Establishing (< 50 worker ants per tree), transient (50–200), established (> 200) (summarized in Hölldobler and Wilson 1990; terms of the functional categories coined by the authors of the current article).

Herbivores.—An unidentified *Contarinia* sp. (Diptera: Cecidomyiidae) induces pinnule-shaped galls in *A. cornigera* at the leaf base, rachis plus petiole, pinna or extrafloral nectaries. Another type of gall is also found on the stems of the acacia trees, but the inducer was not identified. No information is available in the literature about either of the gall-inducers and their biology.

METHODS

Study sites.—The study was carried out about one kilometer northwest of the Los Tuxtlas Biological Station of the National University of Mexico, Veracruz, Mexico (95°04′W and 18°30′N). The Los Tuxtlas region constitutes the northernmost limit of tropical rain forest in the New World (Dirzo and Miranda 1991). The average annual rainfall is 1,966 mm, of which 80% occurs from June to October. December through May is relatively dry (Soto 1976). The study site was an extensively managed pastureland by the forest edge with an area of

approximately 8 hectares. *Acacia* trees were abundant in the pasture, and had been periodically cut. New sprouts growing from the stumps were common. A few larger trees were also present. Sampling was mainly done within a 50 by 30 m plot. Several additional trees along a main road by the studied pasture and along forest trails around the field station were included in the study.

Estimation of infestation rate of host trees with gall-makers.—In total, 85 trees were surveyed to examine the infestation rates from the gall-makers. Both the leaf galls and the stem galls per tree were counted. To verify the presence of ant colony on each tree, thorns of all trees were opened until ants were found or all thorns had been opened and no ant was found.

Examining the relationship between gall density and ant abundance.—Twelve trees from the pasture plus one tree along the road were selected to determine whether gall density and ant density were correlated. Measurements, for each tree, included 1) the number of thorns, 2) the number of thorns occupied by ants, 3) the number of leaf galls, and 4) the number of stem galls. Because old thorns that have been abandoned by ants do not have a leaf at their base, we used the total ant-occupied thorns as an estimate of the number of leaves per tree. Between two to four (mostly three) average-sized thorn pairs were sampled from each tree and the number of ant workers was counted. The average number of ants per thorn was then multiplied by the number of ant-occupied thorns of the tree to calculate the ant colony size. The ant colonies of acacia trees were grouped according to Janzen's classification (1967) into three functional categories: Establishing (< 50 ants per tree), transient (50–200), established (> 200) (summarized in Hölldobler and Wilson 1990).

Examining the distribution pattern of leaf galls and parasitism.—Leaves were sampled from a set of 17 trees to document the distribution of leaf galls on the trees and

incidence of parasitism of these galls by parasitic wasps. Two of these trees were growing along the road, one was close to the research station, and the others were from the pasture. On each tree, all leaves with mature galls were collected, bagged separately, labeled, and brought back to the laboratory for dissection. Gall size (width across the middle), the number of galls, and the positions of galls were recorded for each leaf. Galled leaves were classified as being galled at leaf base, rachis plus petiole, pinna, or extrafloral nectary (hereafter BAS, RACH, PINN, and NECT respectively). Only galls with a direct connection with a nectary will be classified as being galled at extrafloral nectary. The few leaves (n = 2) that were galled at more than one position were not included in the analysis. Occurrences of parasitism and predation were also recorded. Parasitism was determined by counting the number of galls with exit holes by parasitic wasps and/or the number of galls with parasitic wasp larvae or pupae still remaining. Predation was estimated by counting the number of galls that had been broken open.

Voucher specimens of the leaf gall-inducer are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (Dr. Gagné) and in the senior author's collection, and of the parasitoids in the National Museum of Natural History, Smithsonian Institution, Washington, DC (Dr. Schauff).

Results

The leaf gall induced by *Contarinia* sp. consists of a basal larval chamber in the stem, petiole, rachis, or pinna, and an upper part that resembles a pinnule in shape and color. A single developing larva feeds within the basal larval chamber, moves up into the pinnule-like part as a mature larva, and pupates there. Galls crack at the tip when mature and the adult midges emerge. The exit holes of the parasitoids were round and made at the lateral side of the pinnule-like upper part of the gall.
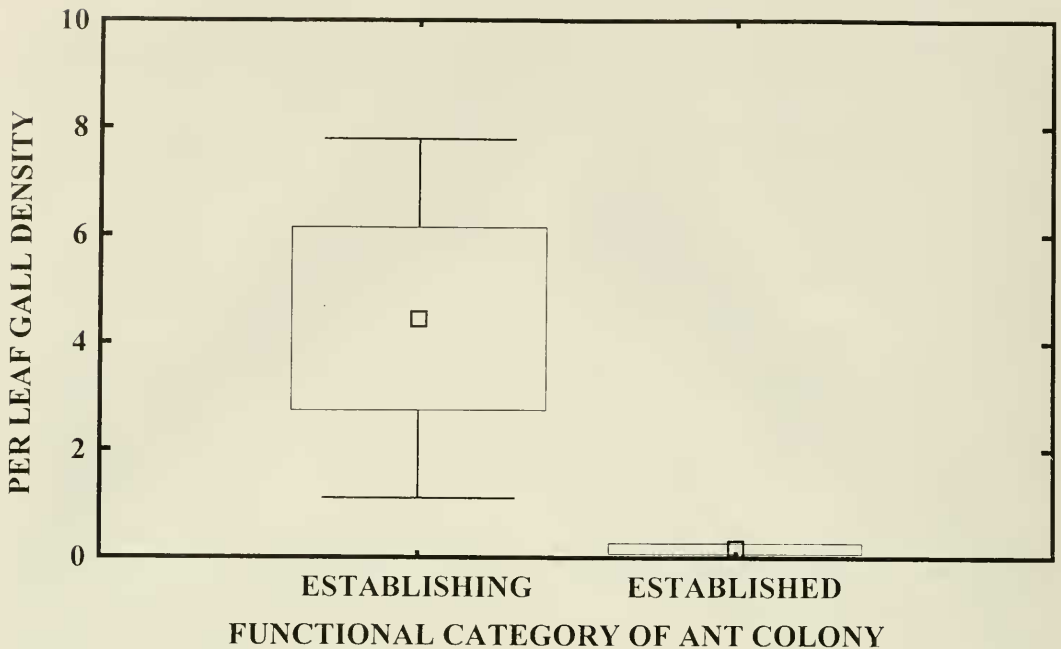
Fig. 2.   The per leaf gall density of galls caused by *Contarinia* sp. is different between trees with establishing (n = 6) and established (n = 7) ant colonies (Mann-Whitney U-test, *P* = 0.01, U = 2.00). Shown is sample mean (inner rectangle) ±1.00 standard error (outer rectangle), and ±1.96 standard error (parallel horizontal lines).

The stem gall is an inconspicuous swelling with larvae living in larval chambers in the woody part of the stem. The larvae dissected out of the stem galls could not be identified to genus, although it is clear that it does not belong to *Contarinia*.

Two and one species of parasitoid wasps were reared from the leaf galls and the stem galls, respectively. The two species reared from the leaf galls are *Closterocerus* sp. (Eulophidae) and *Eurytoma* sp. (Eurytomidae). The parasitic wasps reared from the stem galls belong to a unidentified genus of Tanaostigmatidae (Chalcidoidea), a family whose members are generally gall-inducers with one species known as parasitoid (Gibson 1993).

More than half of all *A. cornigera* trees studied were found to have leaf galls (61.2%). Overall leaf gall density per tree was 9.56 (n = 85, X_{max} = 95, SD = 16.52). Slightly more than half of all host trees had stem galls (51.8%). Stem gall density per tree was 2.18 (n = 85, X_{max} = 18, SD = 3.53). All trees checked for ant presence in the study (n = 85) were found to host *P. ferrugineus* colonies. Only two functional categories of ant colony, Establishing and established, were found on the studied trees.

The average number of galls per leaf of each tree was not significantly related to the size of the ant colony in terms of the number of worker ants inhabiting the tree (*P* = 0.10, r^2 = 0.22), but differed significantly between the trees that host establishing ant colonies and those that host established ones (Mann-Whitney U-test, *P* = 0.01, U = 2.00) (Fig. 2). The number of stem galls per tree was not related to ant colony size (*P* = 0.25, r^2 = 0.12), nor to the functional categories of ant colony (Mann-Whitney U-test, *P* = 0.22, U = 12.5).

Galls were unevenly distributed among galling positions within a leaf. Galls were more often found on the rachis and pinna
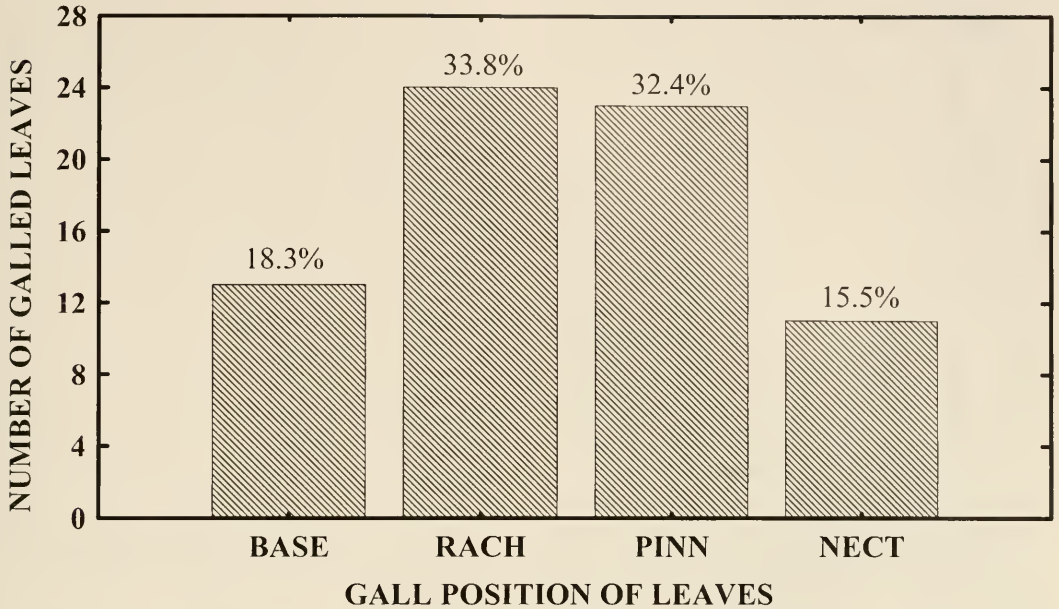
Fig. 3.   Observed proportion of leaves galled by *Contarinia sp.* on different positions. The galled leaves were classified into four types according to gall forming positions of a leaf: at leaf base (BASE), at rachis (RACH), at pinna (PINN) and at extrafloral nectary (NECT). χ^2-test showed that galls were unevenly distributed ($P < 0.05$, $\chi^2 = 8.70$, df = 3).

than on extrafloral nectaries or at the leaf base ($\chi^2 = 8.70$, $P < 0.05$, df = 3) (Fig. 3). Leaf gall size differed significantly among positions of gall formation ($P = 0.01$). Galls formed on extrafloral nectaries or at the leaf base were larger than those formed at the rachis or pinna (Fig. 4).

The overall parasitism rate was 12.3% (n = 382). No difference in parasitism of leaf galls was found among gall-forming positions (One-way ANOVA, F(2, 68) = 0.695, $P = 0.55$), or between *A. cornigera* trees hosting ant colonies of different functional categories (Mann-Whitney U-test, $P = 0.77$, U = 7.0). Data on parasitism of stem galls were not sufficient for statistical analysis.

Predation on leaf galls was generally low: only 3.9% of the 382 sampled leaf galls were observed to have been bitten open by predators, apparently by other insects. No predation was observed on stem galls.

DISCUSSION

Even though all *A. cornigera* trees surveyed were colonized by *P. ferrugineus,* gall midge infestation rates were rather high, suggesting that the gall midges can somehow circumvent the ant defense.

The per leaf density of *Contarinia* galls of each tree was not related to the ant colony size in terms of the number of worker ants. There does appear, however, to be a significant relationship between per leaf gall density of each tree and the functional categories of ant colonies found on the trees. This indicates that ant protection does reduce gall density. It also suggests that the degree of biotic protection for the trees is likely to be affected by the socially initiated behavior of the protecting ant colony. During the Establishing stage, the ant workers are less active and the protection is weak. When the ant colony becomes large and the workers are more aggressive, ant protection becomes more intensive. We did not find
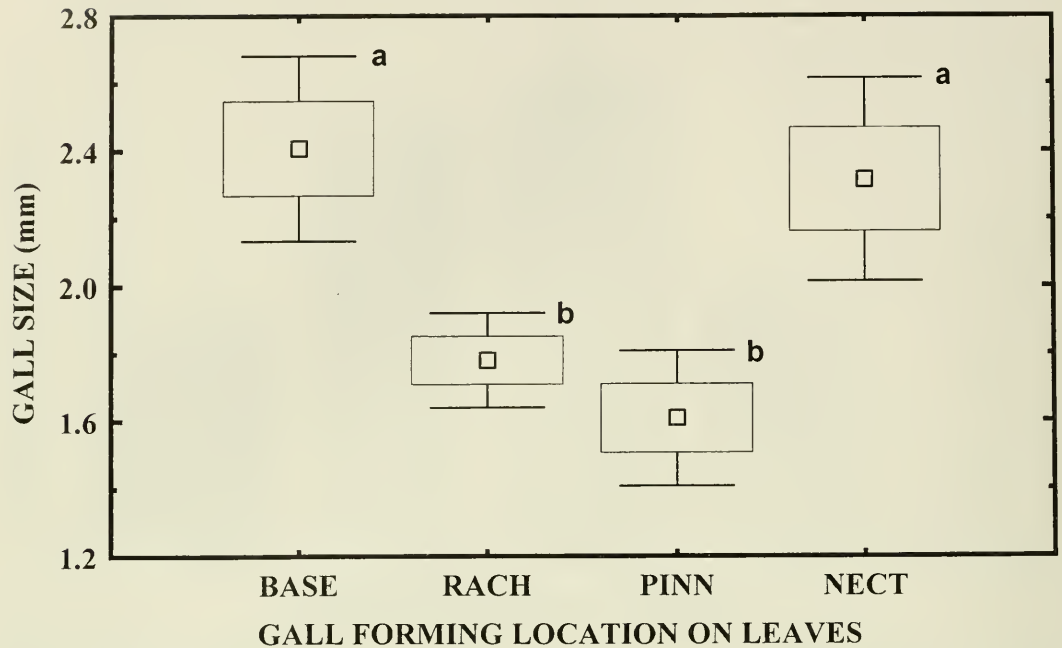
Fig. 4.   Comparison of average size of galls induced by *Cnotarinia sp.* on ant acacia leaves at different gall-forming positions. Samples with different letters at upper left are significantly different using the Newman-Keuls Test (*P* = 0.01). The galled leaves were classified into four types according to gall forming positions of a leaf: at leaf base (BASE), at rachis (RACH), at pinna (PINN) and at extrafloral nectary (NECT).

similar results for the per tree density of stem galls between trees hosting different functional categories of ant colonies. It is likely that the stems are less important to the ants as a food resource and less frequently visited. Therefore the activity of the stem gall midge is less likely to be affected by ant activities in terms of the size and development stage of the ant colonies.

Galls suffered very little predation. Heads and Lawton (1985) observed that ants on bracken (*Pteridium aquilinum*) were attracted to the extrafloral nectaries and protected the plant from caterpillars by attacking them. The ants, however, appeared to have no effect on the two species of gall midges that induce galls on bracken pinna because the midges were concealed inside the galls.

The fact that more leaves were found with galls at the rachis and pinna than at the leaf base or the extrafloral nectaries may indicate that the egg-laying female of *Con-*

tarinia sp. prefers the former sites. However, it does not seem to be beneficial for her offspring to develop at such sites because those galls were significantly smaller than those at the nectaries and leaf base. In general, large galls result in high fecundity (Weis et al. 1988) and better protection from natural enemies (Price and Clancy 1986, Weis et al. 1988). Thus it does not seem to be an adaptive behavior for the ovipositing female midge to prefer rachis and pinna for egg-laying, unless they are attacked by ants at the other sites.

One alternative explanation for the uneven distribution pattern of galls on leaves is that egg-laying females, eggs and young larvae at leaf bases and extrafloral nectaries are subject to more intense predation than those at the rachises. The acacia tree is protected by the ant because it provides nesting thorns, Beltian bodies and extrafloral nectars. The exclusion of herbivores from ant-acacia tree by the ants is in fact the result

of resource competition, which can become more intense if it is a direct one. For example, when an extrafloral nectary is galled by the leaf gall midge, it can no longer function as a nectar provider. Therefore, the ant workers should chase away the egg-laying female gall midge from extrafloral nectaries, and actively remove eggs and unencapsulated larvae. Acacia thorns, as we observed, were excavated at very young stages by the ant, and are thus under ant protection from the very beginning. The proximity of the leaf base to the thorns will expose an egg-laying female of *Contarinia* sp. and her offspring to a higher risk compared to the other positions. Therefore, the gall midge female may prefer to lay her eggs on the rachis and pinna rather than at the leaf base or the extrafloral nectary, thus creating the uneven distribution pattern of galls. Alternatively, she may not demonstrate a preference for a particular oviposition site, but the different degrees of ant predation create the pattern. It is also possible that a combination of both takes place.

We found no difference in the rate of parasitism of galls on trees with different degrees of ant protection derived from functional categories of ant colony, or among positions within leaves. Other studies have shown herbivores on plants defended by ants to be less frequently parasitized than those on plants without ants, and concealed feeders to be parasitized less frequently in areas of high ant activity (reviewed in Koptur 1992). In our study, the acacia trees with established ant colonies were taller and had more branches, and thus had more available extrafloral nectaries. It is possible that the many nectaries attract more parasitoids (cf. Koptur 1991). Thus, a larger number of parasitoids may circumvent the ant protection for the leaf galls. An alternative explanation is that the parasitoids are highly specialized and are not affected by the ants. Regardless of the explanation, the 'enemy-free space' for the *Contarinia* gall midge in ant protected acacia trees does not seem to exist in terms of parasitic wasps in the present study.

In conclusion, because galls were found on so many ant-colonized acacia trees, data from this study supports the theory that concealed herbivores such as gall-making insects can circumvent ant attack. Because the incidence of galls was much lower on trees hosting established colonies of aggressive ants, this study also indicates that ant protection for the ant-acacia could be effective even against highly specialized herbivores like the *Contarinia* leaf gall midge in the present system. A trade-off may exist for the gall midge in that gall size is largest at leaf positions where risk of predation is greatest. Finally, based on evidence of parasitic wasps in this system, the *Contarinia* leaf gall midge does not appears to enjoy 'enemy-free space' on ant-protected acacia trees.

der, and an anonymous reviewer have helped to improve the manuscript significantly.

Literature Cited

Dirzo, R. and A. Miranda. 1991. Altered patterns of herbivory and diversity in the forest understory: A case study of the possible consequences of contemporary defaunation, pp. 273–287. *In* Price, P. W., T. W. Lewinsohn, G. W. Fernandes, and W. W. Benson, eds. Plant–Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions. John Wiley & Sons, Inc. New York, NY.

Eubanks, M. D., K. A. Nesci, M. K. Petersen, Z. Liu, and H. Bonfil. 1997. The exploitation of an ant-defended host plant by a shelter-building herbivore. Oecologia 109: 454–460.

Fiala, B., U. Maschwitz, and T. Y Pong. 1991. The association between *Macaranga* trees and ants in South-east Asia, pp. 263–270. *In* Huxley, C. and D. Cutler, eds. Ant–Plant Interactions. Oxford Univ. Press, New York.

Fonseca, C. R. 1994. Herbivory and the long-lived leaves of an Amazonian ant-tree. Journal of Ecology 82: 833–842.

Fowler, H.G. 1993. Herbivory and assemblage structure of myrmecophytous understory plants and their associated ants in the central Amazon. Insectes Sociaux 40(2): 137–145.

Futuyma, D. J. 1986. Evolutionary Biology, 2nd edition. Sinauer Associates, Sunderland, Massachusetts.

Gagné, R. J. 1989. The plant-feeding gall midges of North America. Cornell University Press, Ithaca, NY.

Gibson, G. A. P. 1993. Superfamilies Mymarommatoidea and Chalcidoidea, pp. 570–655. *In* Goulet, H. and J. T. Huber, eds. Hymenoptera of the World: An Identification Guide to Families. Research Branch Agriculture Canada Publication 1894/E.

Heads, P. A. and J. H. Lawton. 1985. Bracken, ants and extrafloral nectaries. III. How insect herbivores avoid ant predation. Ecological Entomology 10: 29–42.

Hölldobler, B. and E. O. Wilson. 1990. The Ants. Harvard University Press, Cambridge, Massachusetts.

Huxley, C. and D. Cutler. 1991. Ant–Plant Interactions. Oxford Univ. Press, New York, NY.

Janzen, D.H. 1966. Coevolution of mutualism between ants and acacias in Central America. Evolution 20: 249–75.

———. 1967. Interaction of the Bull's-Horn acacia (*Acacia cornigera* L.) with one of its ant inhabitants (*Pseudomyrmex ferruginea* F. Smith) in eastern Mexico. Kansas University Science Bulletin 47: 315–558.

———. 1974. Swollen-thorn Acacias of Central America. Smithsonian Contributions to Botany 13: 1–131.

Jolivet, P. 1991. Ants, plants and beetles: A triangular relationship, pp. 397–406. *In* Huxley, C. and D. Cutler, eds. Ant–Plant Interactions. Oxford Univ. Press, New York, NY.

Koptur, S. 1991. Extrafloral nectaries of herbs and trees: Modeling the interaction with ants and parasitoids, pp. 213–230. *In* Huxley, C. and D. Cutler, eds. Ant–Plant Interactions. Oxford Univ. Press, New York.

———. 1992. Extrafloral nectary-mediated interactions between Insects and plants, pp. 81–129. *In* Bernays, E., ed. Insect–Plant Interactions IV, CRC Press, Boca Raton, Florida.

Krebs, C. J. 1994. Ecology: The experimental analysis of distribution and abundance, 4th edition. HarperCollins, New York.

Loeffler, C. C. 1996. Adaptive trade-offs of leaf folding in *Dichomeris* caterpillars on goldenrods. Ecological Entomology 21: 34–40.

Longino, J. T. 1991. *Azteca* ants in *Cecropia* trees: Taxonomy, colony structure, and behaviour, pp. 271–288. *In* Huxley, C. and D. Cutler, eds. Ant–Plant Interactions. Oxford Univ. Press, New York.

Mintzer, A. C., H. J. Williams, and S. B. Vinson. 1987. Identity and variation of hexane soluble cuticular components produced by the acacia ant Pseudomyrmex ferruginea. Comparative Biochemistry and Physiology 86B: 27–30.

Price, W. P. and K. M. Clancy. 1986. Interactions among three trophic levels: Gall size and parasitoid attack. Ecology 67: 1593–1600.

Rehr, S. S., P. P. Feeny, and D. H. Janzen. 1973. Chemical defense in Central American non-ant-acacias. Journal of Animal Ecology 42: 405–416.

Seigler D. S., J. E. Dunn, E. E. Conn, and G. L. Holstein. 1978. Acacipetalin from six species of Acacia of Mexico and Texas. Phytochemistry 17: 445–446.

Seigler D. S. and J. E. Ebinger. 1995. Taxonomic revision of the ant-acacias (Fabaceae, Mimosaceae, Acacia, Series Gummiferae) of the new world. Annals of the Missouri Botanical Garden 82: 117–138.

Soto, E. M. 1976. Algunos aspectos climaticos de la region de los Tuxtlas. *In* Gomez-Pompa, A. et al., eds. Regeneracion de Selvas. Compania Editorial Continental, Mexico City, Mexico.

Stephenson, A. G. 1982. The role of the extrafloral nectaries of *Catalpa speciosa* in limiting herbivory and increasing fruit production. Ecology 63: 663–669.

Ward, P. S. 1989. Systematic studies on Pseudomyrmecine ants: revision of the *Pseudomyrmex oculatus* and *P. subtilissinus* species groups, with

taxonomic comments on the other species. Quaestiones Entomologicae 25: 393–468.
———. 1993. Systematic studies on *Pseudomyrmex* acacia-ants (Hymenoptera: Formicidae: Pseudomyrmecinae). Journal of Hymenoptera Research 2: 117–168.

Weis, A. E., R. Walton, and C.L. Crego. 1988. Reactive plant tissue sites and the population biology of gall makers. Annual Review of Entomology 33: 467–86.
Zar, J. H. 1984. Biostatistical Analysis, 2nd edition. Prentice-Hall, Englewood Cliffs, New Jersey.